Endophytic Yeasts: Biology, Ecology and Applications

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Abstract While the study of bacteria and filamentous fungi that inhabit plants has been extensive, endophytic yeast biology remains less understood. Recent research is encouraging as to the potential of endophytic yeasts for industrial and agricultural applications, providing strong incentives for better understanding these yeasts. Endophytic yeasts could have significant advantages over bacterial and filamentous endophytes and they can easily be cultured, stored long term and applied to crops. While more research and especially field trials are required to assess their potential, it seems the use of endophytic yeasts could be a viable way of reducing fertilizer and water inputs in agriculture, and potentially increasing yields. Their application seems especially promising in the field of remediation of heavy metal pollutants, and as biocontrol agents to protect plants from pathogens. However, many aspects of endophytic yeast biology still need to be elucidated, especially when it comes to how the yeasts are able to colonize their niche. This chapter reviews recent research on endophytic yeasts and points to the need for further research into the ecology of these valuable yeasts.

1 Introduction

While the study of endophytic bacteria and filamentous fungi has been extensive, endophytic yeast biology and ecology remain poorly understood. Whether this is due to bias in isolation and cultivation techniques towards bacteria and filamentous fungi, or simply a lesser prevalence of yeasts in the phytobiome, is unclear. This apparent rarity could also be exacerbated by the complex and cryptic nature of their life styles, especially in the case of basidiomycetous yeasts. However, yeasts present many advantages for agricultural use over filamentous fungi given their simpler cultivation and application techniques. Yeasts applied to plants seem to be

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distributed systemically, unlike some filamentous fungi, and can be easily cultivated in a similar way to bacteria. They also present advantages over bacteria including their ability to be freeze-dried more efficiently than bacteria and therefore be more easily distributed for agricultural use. Given their ubiquitous presence in the phytobiome and their potentially great agricultural and industrial applications, it is crucial to further study endophytic yeasts. This chapter reviews recent research on endophytic yeasts and points to the need for further research into the ecology of these valuable microorganisms.

2 Defining Endophytic Yeasts

Here we define endophytic yeasts as fungi that have a unicellular part of their lifecycle, which typically reside within plant tissues and do not cause damage to their hosts. The divide between epiphytic and endophytic yeasts has remained blurred, especially in the case of yeasts that populate fruit surfaces, and could potentially penetrate the outer layer of fruits. However, several groups have reported their confidence in surface sterilization techniques, reporting a lack of epiphytes in the washing media after surface sterilization (Prior et al. 2017; Tantirungkij et al. 2015).

Different hypotheses describing the typical composition of the endophytic yeast community published recently point to diverging views over this issue. This is likely in part due to the large variation of endophytic communities based on the host plant as well as various biotic and abiotic factors (Prior et al. 2017). Opinions differ especially over whether the phytobiome is dominated by the commonly known and studied ascomycetous yeasts or the more cryptic basidiomycetous yeasts. One school of thought claims that, given that ascomycete fungi are more common in endophytic filamentous fungi communities and in the world as a whole, endophytic yeasts must be mostly ascomycetes (Prior et al. 2017). This claim is supported by the fact that basidiomycetes are strict aerobes and therefore ascomycetes may be more successful in microaerobic environments inside plant tissues or fruits (Glushakova and Kachalkin 2017). However, there have been reports of a strong prevalence of basidiomycetous yeasts in plant tissues including in the leaves of *Ficus* plants (Solis et al. 2014). Some might propose that these recent results may be due to a cultivation bias in favor of basidiomycetes. However, this hypothesis was supported by a culture independent approach used for rice leaf yeasts, which also showed that more than half of the reported phylotypes were previously unknown, pointing to the flaws of relying solely on culturing methods for characterizing endophytic yeast communities (Tantirungkij et al. 2015). One point supporting the basidiomycetous-dominated hypothesis is the fact that basidiomycetes have a larger metabolic diversity which could allow them to adapt better to the *in planta* environment (Ichinose 2013). Regardless, these differing hypotheses support the need for further research using high throughput culture-independent sequencing approaches in order to better understand endophytic yeast diversity and prevalence.

3 Plant Growth-Promoting Characteristics

The majority of our knowledge of plant growth-promoting characteristics of endophytes comes from studying bacterial endophytes and comparisons can be useful for studying endophytic yeasts. This hints at evidence of convergent evolution of habitat use between yeasts and bacteria that occupy the phytosphere. This is understandable from their similar lifestyles in terms of their ecological niches, as well as their physiology, including their single-celled existence adapted to aquatic environments, fast growth rates, and the importance of biofilms in their lifecycle. Additionally, there has been evidence indicating the possibility of mixed biofilm formation containing both bacteria and yeasts (Bandara et al. 2006; Firrincieli et al. 2015). These convergent traits, as well as ecological and physical proximity, seem to indicate the possibility of cross-kingdom horizontal gene transfer events. These events have been hinted at in the past but little conclusive evidence has been found as of yet (Firrincieli et al. 2015; Hall et al. 2005; Marcet-Houben and Gabaldon 2010).

Several growth-promoting traits are commonly found in endophytic yeasts and endophytes in general including phytohormone production, stress alleviation, protection against pathogens and increasing nutrient uptake by the plant. All of these traits have been found in yeasts but three stand out in particular as being common to endophytic yeasts, and seem to be unifying characteristics. These are IAA production, siderophore production and ACC deaminase activity.

Plant hormone production provides a direct method of plant growth promotion by endophytes. Auxins and gibberellins have many growth-promoting properties in plants including promoting root growth and stem elongation, as well as more broadly, cell proliferation and elongation. Specifically, the production of indole-3-acetic acid (IAA) by endophytic yeasts has been widely reported by several groups and extensively reviewed (Doty 2013; Moller et al. 2016; Nassar et al. 2005). Interestingly, this trait was reported to only occur in media supplemented with tryptophan (Hardoim et al. 2008; Xin et al. 2009). This also seems to be true in the case of endophytic bacteria (Kandel et al. 2017). This observation provides a strong basis for the plant endophyte symbiosis. Tryptophan is a complex amino acid which is costly to produce for the yeast but is found inside the plant and in plant exudates (Kamilova et al. 2006). While it may be too costly for the yeast to produce tryptophan to make IAA on its own, when the plant provides it with tryptophan, the yeast can, in return, provide IAA and subsequently promote the growth of its host. This also serves as an indirect way for the plant to divert nitrogen into root and shoot mass, especially in situations where nitrogen is plentiful.

ACC, or 1-aminocyclopropane-1-carboxylate, is a molecule that serves as a precursor to the production of ethylene, a plant stress hormone. ACC deaminases are enzymes that cleave the molecule ACC into α-ketobutyrate and ammonia and have commonly been found in endophytic bacteria, as well as endophytic yeasts (Glick et al. 2007; Nutaratat et al. 2014; Sun et al. 2009). The endophytic yeasts that have this activity may therefore serve as sinks for ACC, therefore decreasing total ethylene concentrations in the plant. Ethylene is a stress hormone that inhibits growth of the plant. Yeasts may therefore prevent this growth inhibition, and generally increase the plant's tolerance to stress. These enzymes may also serve as a mechanism for ammonia secretion by the yeasts, which have been reported in the past and could serve as a way for the plant to recycle nitrogen using its symbiotic partners (Nutaratat et al. 2014).

Siderophore production is another common trait of endophytic yeasts that has been substantially reviewed for arboreal endophytes and found in rice and sugar cane leaf endophytes (Moller et al. 2016; Nutaratat et al. 2014). Siderophores are iron chelating compounds microorganisms produce when facing iron starvation (Loaces et al. 2011). These compounds are secreted and then recaptured once they have chelated iron. This could serve as a method for plant growth promotion as they could provide the plant with chelated iron that it cannot absorb directly from the soil. Additionally, these compounds could help endophytic yeasts colonize the plant and exclude other microorganisms and could explain antifungal characteristics of some yeasts as described later in this review. This is well known in epiphytic yeasts, which prevent fruit spoilage, for example (Loaces et al. 2011; Nutaratat et al. 2014).

Several other plant growth-promoting characteristics have been reported recently but less commonly, possibly as a result of a lack of in depth characterization of these endophytes. One of these characteristics is catalase activity, an enzyme that decreases the presence of reactive oxygen species and could help promote stress tolerance in the plant (Khalifa et al. 2016). This catalase activity has been reported recently in many of the yeast endophytes found in sugar cane and rice leaves in Thailand (Nutaratat et al. 2014). Nutaratat et al. also reported ammonium secretion independent of ACC deaminase activity, as well as increased phosphate solubilization by several of the yeasts. Additionally, the production of polyamines by these yeasts was also reported. These compounds have a complex role in plant growth and are involved in many cellular processes including the synthesis of macromolecules, as well as growth, survival and stress tolerance of cells. However, they could also generally function in plant growth promotion by yeasts (Takahashi and Kakehi 2010).

4 Industrial and Environmental Applications

Given the growth-promoting characteristics of endophytic yeasts, their potential applications in agriculture are great. Growth promotion by a poplar endophyte *Rhodotorula graminis* has been reported in bell peppers and poplar (Khan et al. 2012; Knoth et al. 2013). Additionally, another *Rhodotorula* strain has been shown to increase germination of cucumber seedlings both through inoculation and treatment by filtered supernatant (Akhtyamova and Sattarova 2013). However, very few of these plant experiments exist as most of the research in the past has been focused on the diversity and ecology of these yeasts rather than their applications.

The use of these yeast endophytes in agriculture could reduce inputs of water and fertilizer and are important to study in the future given our growing population and increasing food demand.

A couple of the studies that showed growth promotion by endophytic yeasts focused on their potential to be used for bioaugmented phytoremediation of heavy metals. Heavy metal contaminated sites pose significant health risks and current technologies for remediation are expensive and insufficient (Deng et al. 2012; Dhankher et al. 2012). Although decontamination using plants as bioaccumulators offers a cheaper alternative that could provide potential for concurrent bioenergy production, this strategy is often inefficient given that heavy metals negatively affect plant health (Deng et al. 2012; Sheng et al. 2008). However, these negative impacts on plant health could be remediated by the addition of pollutant tolerant endophytes, termed bioaugmented phytoremediation. Deng et al. reported that a *Cryptococcus sp.* from rape roots not only increased the survival rate of Chinese kale seedlings in metal contaminated soil but also promoted their growth. Additionally, Wang et al. showed that *Brassica sp.* seedlings inoculated with endophytic *Rhodotorula sp.* showed increased growth and increased extraction of Cd, Pb, Zn, and Cu (Wang et al. 2013). In addition to the previously discussed advantages of using endophytic yeasts over bacteria, yeasts may also be better suited for bioaugmented phytoremediation given that contaminated sites are often contaminated by multiple organic and inorganic pollutants and fungi tend to have a broader range of tolerances to pollutants (D’Annibale et al. 2006; Deng et al. 2012).

Another promising use of endophytic yeasts in agriculture is their use as biocontrol agents against fungal and bacterial pathogens. This use of endophytes for biocontrol has been reported many times for bacterial endophytes (Ait Barka et al. 2002; Brooks et al. 1994; Compant et al. 2005; Kandel et al. 2017; Miotto-Vilanova et al. 2016). Conversely, the use of endophytic yeasts as potential biocontrol agents has not been studied until very recently. One group reported that a *Rhodotorula rubra* strain, isolated from rice, showed strong inhibition of various *Fusarium* species, which are one of the most economically important fungal pathogens (Akhtyamova and Sattarova 2013). Additionally, the yeast also showed strong inhibition of growth of *Xanthomoonas malvacearum* and *Erwinia* species, both important bacterial plant pathogens. This biocontrol ability was also found in the filtered supernatant of the yeast (Akhtyamova and Sattarova 2013). Additionally, Kandel et al. reported the antifungal activity of the poplar endophyte *Rhodotorula graminis* against the common fungal pathogen *Rhizoctonia solani* (Kandel et al. 2017).

There are a few hypotheses that explain the potential mechanisms of these biocontrol abilities. One involves the production of siderophores described earlier in this review. In addition to their potential role to promote plant growth, siderophores that scavenge and sequester iron could prevent the establishment of fungal pathogens since other fungi need iron in order to grow and establish. This has been shown in epiphytic yeasts and bacteria (Calvente et al. 2001; Loaces et al. 2011). However, antifungal characteristics have been found in yeasts that do not produce siderophores. These antifungal characteristics seem to be fairly uncommon which points to a more specific mechanism (Nutaratat et al. 2014). A likely hypothesis is the secretion by endophytic yeasts of cellulases and cell wall degrading enzymes, described as the killer yeast phenomenon (Magliani et al. 1997). Some yeasts produce toxins that have strong antagonistic effects on other fungi and bacteria and likely phytopathogens which could help protect their host (Magliani et al. 1997). Finally, endophytic yeasts might help exclude phytopathogens simply by occupying their niche, thus preventing deleterious fungi and oomycetes from colonizing plant tissues (Prior et al. 2017).

Endophytic yeasts could also be used for the production of a variety of biochemicals as was previously reviewed (Doty 2013). Possessing a wide variety of metabolic options given their adaptations to fluctuations in their environments and their wide host range, endophytic yeasts could provide opportunities for more efficient metabolism of various, difficult to produce, chemicals.

5 Anthropogenic Impacts on Endophytic Yeast Diversity

Recently, there has been increased interest in the research of the anthropogenic impacts on yeast diversity. Notably, Prior et al. studied the impact of fungicide on yeast communities. Fungicides are highly toxic to soil communities and cause significant stress to plants (Jorgensen et al. 2012). However, their direct impact on endophytes has not been studied until recently. This group looked closely at the impacts of two types of fungicides, contact fungicides, such as sulfur and copper, and systemic fungicides such as azoxystrobin. Sulfur and copper had a strong effect on the species richness and colony count of common bean endophytes. The systemic fungicide, azoxystrobin, had an even stronger impact on the endophytic community. Interestingly, once the fungicides leached out of the plant host, the niche inside the plant was eventually recolonized. However, this recolonization also represented a drastic shift in species diversity. This may indicate a recolonization of the plant by potentially pathogenic fungi where endophytes lived before, and could hint at an explanation for the variable success of fungicides in some crops.

Another group has focused on the changes in endophytic communities in plants close to urban areas. This group previously reported a stronger presence of human pathogenic and opportunistic yeast species in pollen in urban environments which may be responsible for increased allergic reactions (Glushakova et al. 2015). More recently, they reported significant changes in the endophytic populations of the fruits of *Malus domestica* and *Pyrus communis* (Glushakova and Kachalkin 2017). Notably, there was a significantly greater abundance of the opportunistic human pathogen *C. parapsilosis.* Overall, they reported that the anthropogenic load has significant impacts on fruit in urban areas. One could imagine potentially significant consequences to endophytic yeast communities within plants living in urban areas and endophytes potentially being outcompeted and replaced by non-native species and human opportunist pathogens. This anthropogenic impact has also been reported by Solis et al. who noticed that plants in greenhouses in Berlin that were moved across various locations had a greater diversity of endophytic yeasts as compared to ones that were left in soil throughout the year (Solis et al. 2014). These data point to a strong anthropogenic impact on endophytic yeast communities that may have significant consequences on plant health.

6 Colonization

One of the most intriguing aspects of endophytic yeast biology is the ability of the yeasts to fully colonize plants. Unlike bacteria, yeasts are not motile and do not have chemotactic capabilities towards, for example, plant root exudates. This means that yeasts that are in the soil most likely cannot colonize plants simply by swimming in the direction of the roots like bacteria do. Additionally, they do not typically form a mycelium and therefore, cannot produce hyphae that are able to grow towards their hosts. Epiphytic yeasts, in addition to being passively diffused in their environment by air and water, are dispersed by insects. A couple of specific examples include the vectoring of *Saccharomyces cerevisiae* by social wasps, as well as the sweet potato epiphyte, *Candida kunwiensis,* which has been found on the bumblebees that pollinate the sweet potato plants (Hong et al. 2003; Stefanini et al. 2012). Further research showed that yeasts are strongly associated with insects including in the guts of beetles and on fruit flies (Chandler et al. 2012; Suh et al. 2005). This association was extensively reviewed by Ganter, and supports the convincing hypothesis that endophytic yeasts are vectored by insects and are able to colonize their plant hosts in this way (Ganter 2006). Supporting evidence includes the recent study showing that several endophytic yeasts of rice leaves were also found in association with brown plant hoppers and beetles (Tantirungkij et al. 2015). Additionally, there have been recent studies suggesting the importance of endophytic yeasts in multipartite associations between tree-associated insects, their host trees, and yeasts which were thoroughly reviewed by Moller et al. (2016). Overall, this idea offers a fairly convincing hypothesis of one of the ways endophytic yeasts are able to move around their environment and colonize different plant hosts.

The other important question is how the yeasts can systemically colonize the host plant. The endophytic yeast, *Rhodotorula graminis,* is able to colonize the entire plant, including leaf and xylem tissue when the plant is inoculated from the roots (Kandel et al. unpublished). One simple explanation is that the yeast can colonize the plant passively, simply by growing inside of the root until the population can gain access to the xylem tissue, and from there, colonize the rest of the plant as water is shuttled through the plant. Although this has not been shown directly, as plant associated fungi, endophytic yeasts likely have the enzymatic capabilities to degrade plant cell walls. This has been directly shown in bacterial and filamentous endophytes (Santoyo et al. 2016; Uzma et al. 2016).

Another interesting hypothesis is the possible role of a dimorphic life cycle of some endophytic yeasts. As discussed previously, many endophytic yeasts are basidiomycetes, a phylum which contains many plant and animal pathogens with dimorphic lifecycles including a saprobic yeast phase as well as a sexual filamentous phase (Morrow and Fraser 2009). In particular, *Cryptococcus* and *Rhodotorula*, two genera that are commonly found inside plant hosts, contain many yeast strains with observed filamentous stages.

To give a specific example, *Rhodotorula graminis* strain WP1 is a poplar endophyte that was the first endophytic yeast to have its genome fully sequenced (Firrincieli et al. 2015). According to recent phylogenies, this endophyte is very closely related to *Rhodotorula glutinis var. glutinis* (Biswas et al. 2001). Using a clever experiment with auxotrophic mutants of two different mating types of this species, this yeast was shown to form a mycelium when opposite mating types were mixed together (Banno 1967). Given the evolutionary relationship between the two yeasts, it is extremely likely that *R. graminis* is also able to form a mycelium. This is further supported by recent investigations into the mating locus of *R. graminis* which has a similar structure to *R. glutinis* (Joubert, unpublished). Additionally, genomic analysis by Maia et al. showed strong conservation between the mating locus of *R. gramins* strain WP1 and other closely related species (Maia et al. 2015). These preliminary investigations have strongly supported the presence of two separate mating types of *R. graminis* (Firincelli et al., unpublished). However, the significance of this sexual filamentous stage in yeast colonization needs to be evaluated. These mycelial forms could enable the active spread of the endophyte throughout the plant and allow it to colonize its host from the roots to the leaves. However, this is unlikely to play a significant role in plant colonization given that a large portion of endophytic yeasts are ascomycetes which do not form a filament and the fact that the yeast can seemingly colonize the plant in its haploid yeast stage. One thing is for certain, these filamentous sexual forms are a great source of recombination and diversity, potentially allowing the yeasts to adapt rapidly to different plant hosts and environmental conditions.

Another interesting hypothesis to explain yeast colonization is the role of the production of IAA. This hormone affects plant roots by inhibiting differentiation of plant root cells and promoting root elongation. This could positively affect plant health overall and could also provide opportunities for colonization by yeast endophytes. The main barrier to microbial colonization of the xylem is the Casparian strip in mature roots. However, if the yeast produces enough IAA in the rhizosphere, as they are capable of doing in vitro, it could prevent root cells from maturing, and therefore, decrease the presence of the Casparian strip (Kandel et al. 2017; Verbon and Liberman 2016). This could provide an avenue for colonization by the yeast. Interestingly, ACC deaminase activity also promotes root elongation and therefore might provide a similar benefit to the yeast in colonization (Glick et al. 2007).

A possible requirement to the establishment of a yeast population is the formation of a biofilm. The yeast lifestyle in general is adapted for aquatic environments, such as the plant xylem, but biofilm formation is likely a requirement for full colonization of the xylem by the yeast (Moller et al. 2016). Genes encoding a polysaccharide capsule were also found in the genome of *R. graminis* strain WP1 (Firrincieli et al. 2015). These endophyte biofilms could allow a form of protection from various environmental conditions, as well as a site of reproduction and the formation of resistance stages as they do in other yeasts (Ramage et al. 2009). This could also be a strong source of expression of plant growth-promoting characteristics of these yeasts, and potentially provide an explanation for the paradox of how yeasts are able to fight off fungal phytopathogens using antifungal molecules without harming themselves. Although this has not been directly studied in endophytic yeasts, this theory seems to be supported by evidence that endophytes have stronger endophytic characteristics in mixed biofilms including both bacteria and filamentous endophytes (Bandara et al. 2006).

7 Conclusion

While the biology of endophytic yeasts remains relatively unexplored, recent research is encouraging as to their potential for industrial and agricultural applications. While more research and especially field trials need to be done to assess this potential, it seems the use of endophytic yeasts could be a viable way of reducing fertilizer and water inputs in agriculture, and potentially increasing yields. These yeasts could also have significant advantages over their bacterial and filamentous neighbors. Their application seems especially promising in the field of remediation of heavy metal pollutants, and as biocontrol agents to protect plants from pathogens without harming the plant's microbiome. Still, many questions remain, especially when it comes to the biology and diversity of these yeasts. The way yeasts are able to colonize plants still remains a mystery, and many experiments on the process of inoculation of the host need to be done in order to elucidate this mystery. The role of insects in the life history of yeasts and their dispersal seem to be a promising avenue for research as well. Finally, many questions on the diversity of yeast species across different plant hosts still need to be answered, and the possibility of significant cultivation biases needs to be thoroughly evaluated.

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